

CONVERGENCE IN THE COEREBIDAE

BY WILLIAM J. BEECHER¹

EXTENSIVE efforts of the writer to find a sound anatomical basis for determining the phylogenetic relationships of passerine families leave it clear that the hazard of adaptive convergence in bird systematics has been underestimated. The present analysis of convergence in the neotropical Honey Creepers (family Coerebidae) offers evidence that this is an artificial group. It appears to be composed, in fact, of nectar-adapted warblers (Parulidae) and nectar-adapted tanagers (Thraupidae) that have evolved convergently because of similarity of diet.

The Convergence Hazard in Taxonomy

Sound systematic work in the higher categories demands sound criteria for clearly distinguishing between adaptation and phylogeny. The investigator at this level sees phylogeny through a screen of food and niche adaptations which often obscure true relationships. Such classic cases of convergence between Old and New World groups as were recently reviewed by Friedmann (1946) are obvious and constitute no hazard. But convergence between members of closely related groups occupying the same range may be such that the most expert taxonomists are unable to decide the true affinities on the basis of external characters alone (Beecher, 1950). This is no reflection on the taxonomists, who have generally been the first to recognize the problem, referring such moot groups as the Coerebidae to the comparative anatomist for additional evidence.

But internal characters are not necessarily more reliable than external ones for indicating phylogeny. They are merely additional clues, often of a very conservative sort, but sometimes capable of adaptive changes as rapid as those known for any external features. Sclater (1886: 1) long ago observed that it was "in some instances difficult to distinguish" the Coerebidae from warblers on the one hand and tanagers on the other. Lucas (1894: 299-309) made an anatomical survey of several of the most important coerebid genera; though he considered his findings confusing and inconclusive, they nevertheless confirmed an opinion many times expressed that the group needed study and was probably heterogeneous. Ridgway (1902: 377) obviously regarded the Coerebidae as close to the Parulidae and Thraupidae. He even removed the

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genera *Conirostrum* and *Ateleodacnis* to the Parulidae, whence Lucas (1894: 309-310) had earlier removed *Certhidea*. Both Sclater (1886: 47) and Ridgway (*loc. cit.*) placed *Glossiptila* (*Euneornis*) in a monotypic subfamily under the Coerebidae. Hellmayr (1935: 218-331), however, placed all these genera, except *Certhidea*, in the Coerebidae without subfamilial distinction. Thus there has been a difference of opinion as to the status of certain genera, but a consensus that the family belongs close to the warblers and tanagers.

Convergence in the Coerebidae

It is axiomatic that a family must be erected on a basis of characters common to the included genera, and the assumption is that these characters will be fundamental, expressing a common phylogenetic origin. As pointed out by Mayr (1942: 276) and Simpson (1945: 17), any higher category must be monophyletic. The Coerebidae do not appear to satisfy these requirements.

Examining the characters of the group we find none that really distinguish it. Some species are brilliant in plumage, others dull. The bill is extremely variable—long, short, straight, curved, notched, even hooked—and this diversity of form extends to the tongue and to the head as a whole. The only feature common to all members is the adaptive trait of nectar-feeding. This trait is naturally suspect as a character if the birds involved are to be classified according to common origin. Lucas (1894), in attempting to determine the origins of the family, seized principally upon those features most strongly modified by the nectar-feeding adaptation—bony palate, tongue, and intestine. Ridgway (1902: 375) erred, however, when he stated that Lucas considered the Coerebidae “apparently more nearly related to the Australasian family Meliphagidae (Honey-eaters) than to the American families Mniotiltidae and Tanagridae. . . .” What Lucas did say (1894: 309) was that “the Coerebidae do not form a homogeneous group. . . .” His principal reference to the Meliphagidae (*loc. cit.*) concerned the tongue of *Certhiola*, which he believed to resemble “that of some of the Meliphagidae. . . .”

Evidence of convergence is to be obtained through a careful study of morphology, especially through study of parts of the animal not likely to be modified by the selection pressure bringing about convergence. It is well known that different parts of an animal evolve at different rates (Simpson, 1944). The hind limb is very similar in muscle pattern throughout the order Passeriformes and seems to have become relatively static after attaining a high level of general efficiency. The syringeal musculature, slightly less conservative, has served to divide this large order into suborders. But there is evidence (Beecher, 1951) that the bill and skull are still rapidly evolving in passerines—leading the way in evolution. Having dissected to date nearly a thousand specimens of oscine birds in all families (over six hundred species), the writer finds that the more rapidly-evolving jaw muscle-patterns are clearly different for each

family. When used with the several additional lines of evidence indicated later in this paper they seem to delineate an evolutionary sequence based on adaptation to various food types.

Evidence of Convergence from Jaw Muscle-Patterns

To recognize the family differences in jaw muscle-pattern it is necessary to distinguish between two basic types of skeletal muscle—pinnate and parallel (Pfuhl, 1936). In the parallel type all fibers run the full length of the muscle and exert pull, upon contraction, directly between the points of attachment. The vireos (Vireonidae) typify this pattern (Fig. 1) with nearly the entire

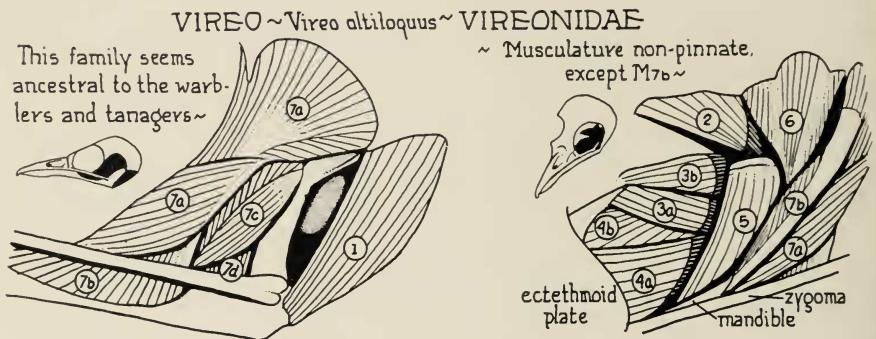


FIG. 1. Jaw muscle-pattern of *Vireo altiloquus* broken down into functional groups. In gaping, *M. depressor mandibulae* (1) depresses the lower mandible, while *M. protractor quadrati* (2) elevates the upper mandible.

The combined action of the palatine retractors 3, 4, and 5 draws the upper mandible downward. The palatine retractors are:

3. *M. pterygoideus dorsalis* (a) anterior; (b) posterior
4. *M. pterygoideus ventralis* (a) anterior; (b) posterior
5. *M. pseudotemporalis profundus*

The combined action of the mandibular adductors 6 and 7 draws the lower mandible upward. The mandibular adductors are:

6. *M. pseudotemporalis superficialis*
7. *M. adductor mandibulae* (a) externus superficialis; (b) externus medialis; (c) externus profundus; (d) posterior

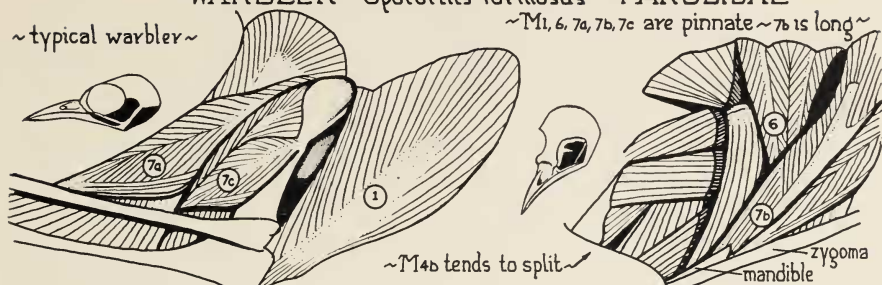
jaw musculature parallel. The pinnate type is one in which the tendon or raphe runs the length of the muscle and the short fibers originate from it as the barbs originate from the shaft of a feather. The warblers show this pattern in *M. pseudotemporalis superficialis* (6) and *M. adductor mandibulae externus superficialis* (7a) as seen in Figure 2 (*Oporornis*). Grant (1942: 384) has pointed out that such a muscle is more efficient, having "a much greater functional cross section for its bulk."

It has appeared to the writer, on the basis of both skull structure and parallel

WARBLER ~ *Oporornis formosus* ~ PARULIDAE

~ typical warbler ~

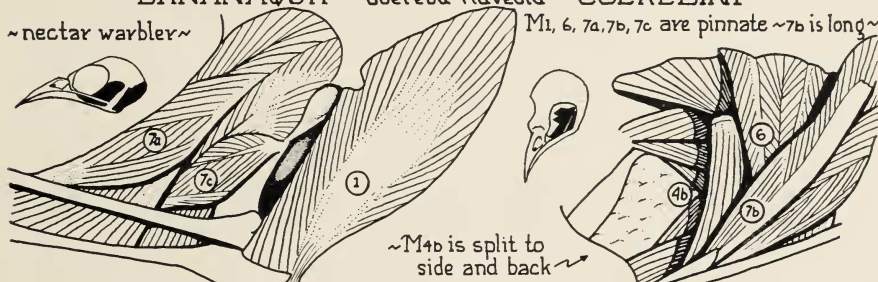
~ M1, 6, 7a, 7b, 7c are pinnate ~ 7b is long ~



BANANAQUIT ~ *Coereba flaveola* ~ COEREBINI

~ nectar warbler ~

M1, 6, 7a, 7b, 7c are pinnate ~ 7b is long ~



HONEY CREEPER ~ *Cyanerpes cyaneus* ~ DACNINI

~ nectar tanager ~

~ Only M6, 7c are pinnate ~ 7b is short ~



TANAGER ~ *Calospiza arthus* ~ THRAUPIDAE

~ typical tanager ~

~ Only M6, 7c are pinnate ~ 7b is short ~

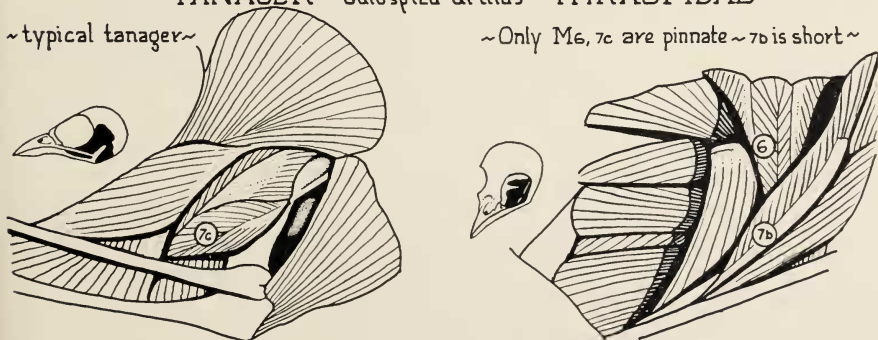


FIG. 2. Comparison of jaw muscle-pattern in typical warblers (Parulidae) and tanagers (Thraupidae) with that of their nectar-adapted forms.

jaw muscle-pattern, that the Vireonidae, like the Old World Monarch flycatchers from which it stems, is composed of phylogenetically primitive insect-eaters (Beecher, unpublished). Distribution patterns suggest that such a type may have existed even prior to the origin of flowering plants in the Upper Cretaceous and that all of the nine-primaried American families stem from ancestral vireos. The lighter, more agile Parulidae appear to have arisen with pinnate adductors of less mass and greater efficiency—a more adaptable group of insect-eaters. The heavier Thraupidae—a group adapted to feed on the abundant fruit of flowering plants—appear to have arisen with somewhat less pinnate adductors. The Parulidae and Thraupidae are, in fact, to be regarded as real adaptive branches on the phylogenetic tree, each having arisen in response to intense selection pressure on the primitive insect-eaters. The importance of the huge food supply furnished by the origin of flowering plants in producing this pressure cannot be over-emphasized. Logically it should come to bear similarly on warblers and tanagers, independently producing nectar-adapted and seed-adapted groups with ever-increasing tendency toward pinnate adductors.

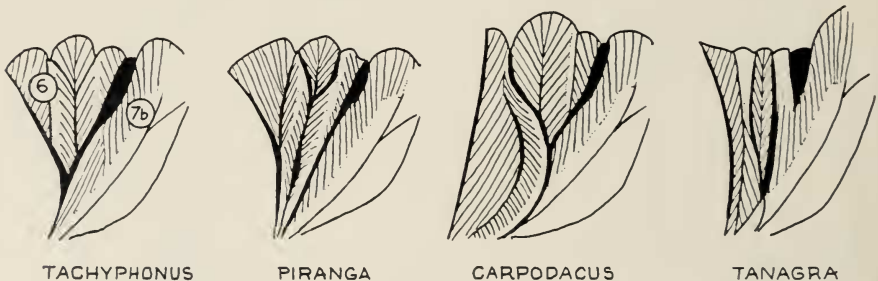


FIG. 3. An apparent shift of muscle fibers from *M7b* to *M6* (from left to right) with increased adducting power in the cardueline line of tanagers.

To argue the question whether the increase in pinnate musculature is phylogenetic or adaptive is academic. It is both, but there is every indication that such advances in jaw muscle-pattern are conservative enough to have phylogenetic value for taxonomic diagnosis at the family level of category. The black-bird family (Icteridae) which appear to have arisen from the emberizine finches via the finch-like Cowbird, *Molothrus* (Beecher, 1951), retains pinnate adductors despite all the food adaptations and accompanying bill changes for which its genera are noted. The muscle-patterns of tanagers and warblers differ from each other and offer a sound basis for taxonomic separation; but, before presenting evidence of convergence in the Coerebidae, it is necessary to emphasize some unusual features of the Thraupidae.

This family, as outlined below, is very large and diverse. Two main lines are distinguishable, leading almost without disjunction to the finch subfamilies

Carduelinae and Richmondeninae. On the basis of jaw muscle-pattern these lines stem from a relatively primitive tanager group comprising *Calospiza*, *Thraupis* and *Ramphocelus*, of which the large genus *Calospiza* is considered by the writer to be the simplest, anatomically, and *Ramphocelus* the most advanced. The latter continues the series into the Richmondeninae in the sequence *Ramphocelus*—*Hemispingus*—*Spindalis*—*Saltator*—*Pitylus*—*Pheucticus*—*Richmondena*. This is not necessarily a direct evolutionary sequence, although it moves in the direction of increasing finch character, especially in the bill and in the heightened pinnate character of *M. adductor mandibulae externus superficialis* (*M7a*), the latter beginning in *Hemispingus* and increasing in the series. There is also good plumage agreement, especially in females, and the horny palate shows an increased tendency to develop a subsidiary lateral ridge, additional to the one so prominent in all tanagers (see *Calospiza*, Fig. 4).

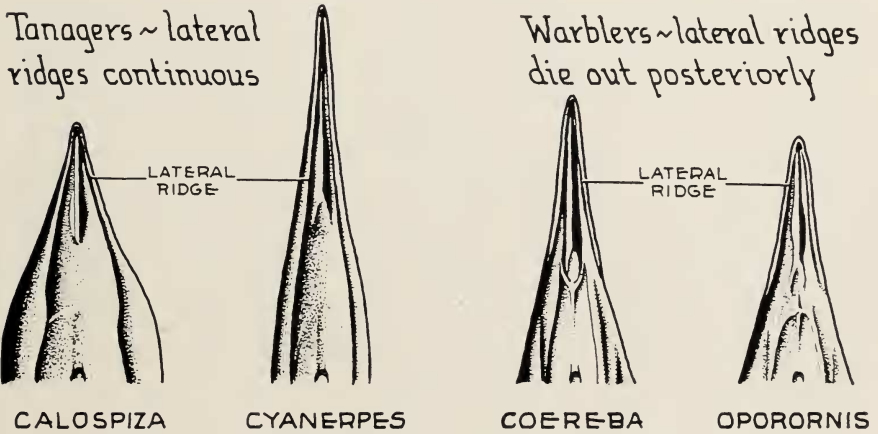


FIG. 4. Comparison of relief pattern seen in the horny palate of typical warblers (Parulidae) and tanagers (Thraupidae) with that of their nectar-adapted forms.

Ramphocelus might, because of its apparent close relationship with *Tachyphonus*, be considered a point of origin for the Carduelinae also—a group quite different in its muscular emphasis. *Tachyphonus* lies at the base of this line. The muscle-pattern of the weak-billed *T. surinamus* is like that of *Ramphocelus*, hence also of *Calospiza* (Fig. 2); but in the heavier-billed *T. rufus* the orbital slip of *M. adductor mandibulae* (*M7b*) is pinnate (Fig. 3). This appears to be correlated with increased adducting power, but with still further increase in the series *Tachyphonus*—*Piranga*—*Habia*—*Tanagra*—*Chlorophonia*—*Stephanophorus*—*Carpodacus* (Fig. 3) there appears to be a shift in emphasis from *M7b* to *M6*. The series terminates in the tremendous forward advance of the latter in *Carpodacus*, which is typical for the Carduelinae as a whole. That this shift involves a transfer of fibers to *M6* is suggested in the sketch of these two mus-

cles for *Tanagra chlorotica* (Fig. 3), where transfer seems to be taking place. The horny palate in this series agrees closely with that of *Calospiza* (Fig. 4), and plumage generally supports the thesis of close relationship.

This digression on the complexities of the Thraupidae is necessary. In no other of the sixty-odd oscinine families do such variations in the muscle-pattern occur. It points up the peculiar fact that the richmondenine finches arise so uninterruptedly out of the tanagers that ornithologists have had to draw the dividing line between the two groups arbitrarily. Now we find the cardueline ("Old World") finches arising also without disjunction from another line of tanagers. *Chlorophonia cyanea*, with a muscle-pattern like that of *Carpodacus*, has a flattened tanager bill. The horny palate of *Stephanophorus diadematus*, a form internally almost identical with *Carpodacus*, has crenulated lateral ridges like those of the plant cutter *Phytotoma*—a further adaptation for bud-eating, so common in the Carduelinae.

Apparently it will be necessary to declare these two groups of tanager-finches subfamilies of the Thraupidae, maintaining another subfamily for the more typical tanagers. It would hardly do to extend the Richmondinae and Carduelinae to include the two generic series cited above as stemming from *Ramphocelus*. Such a grouping would be as arbitrary as the one currently followed and the writer contemplates no change other than the including of the finch groups in the Thraupidae. But it is necessary to recognize that the anatomical modifications terminating in these finch groups have their roots deep in the typical tanagers, the Thraupinae. For this reason the basic muscle-pattern for tanagers is regarded by the writer as that found only in *Calospiza*, *Thraupis* and *Ramphocelus*, though genera not yet dissected by him may be included later. It is this pattern that the writer uses in his present re-examination of the Coerebidae.

A survey of the Vireonidae, here considered as ancestral to both the Parulidae and Thraupidae, reveals a muscle-pattern that is notably non-pinnate. In *Vireo altiloquus* and *V. olivaceus* a suggestion of pinnate character appears in *M. adductor mandibulae externus medialis* (*M7b* in Fig. 1), and this muscle, along with *M7a, c*, and *M6*, becomes fully pinnate in the shrike-like *Cyclarhis* and *Smaragdolanus*. But *Vireo griseus* and *V. flavifrons* lack this suggestion, as do *Hylophilus olivaceus*, *H. hypoxanthus* and *H. decurtatus*. This muscle is short and non-pinnate in the basic muscle-pattern for tanagers such as *Calospiza* but is always long and pinnate in such warblers as *Oporornis* (Fig. 2), *Setophaga*, *Basileuterus*, *Myioborus*, *Granatellus*, *Dendroica*, *Protonotaria*, *Geothlypis*, *Parula*, *Seiurus*, *Mniotilta* and *Icteria*. Thus we see a segregation on the basis of *M7b* that is diagnostic of warblers and tanagers.

Warblers differ from the basic tanagers in having a far more pinnate muscle-pattern, this in spite of the fact that they have much more slender bills and much lighter muscle mass. The pattern seen in *Oporornis* is typical. Pinnate muscles are *M. depressor mandibulae* (*M1*), *M. pseudotemporalis superficialis*

(M6), and three slips of *M. adductor mandibulae*, viz., *externus superficialis* (M7a), *externus medialis* (M7b), and *externus profundus* (M7c). In the basic tanagers only M6 and M7c are pinnate. *M. depressor mandibulae* (M1) is always more highly developed in warblers than in tanagers (Fig. 2).

It was at first puzzling to find both tanager and warbler muscle-patterns appearing in different members of the family Coerebidae. The jaw muscle-pattern of *Coereba flaveola* (Fig. 2) corresponds perfectly, in fact, with that of *Oporornis formosus*, a typical warbler, while that of *Cyanerpes cyaneus* corresponds perfectly with that of *Calospiza arthus*, a typical tanager. It is true that *Coereba* and *Cyanerpes*, in adaptation to nectar-feeding, have an enlarged palatine salivary gland which causes the insertion of *M. pterygoideus ventralis posterior* (M4b) to split into two slips. Even here, however, the manner of the muscle's division is different: in *Coereba* it is split laterally and posteriorly—in *Cyanerpes*, laterally and medially. That this is not simply coincidental is borne out by the fact that, wherever this muscle is split by an enlarged palatine gland in coerebid genera, the disposal of the divided slips is either as in *Coereba* or as in *Cyanerpes*. Intermediate arrangements do not occur.

On the basis of muscle-pattern, then, it would appear that *Coereba* is nothing but a nectar-adapted warbler, and *Cyanerpes* a nectar-adapted tanager. The differences in muscle-pattern and -arrangement may be interpreted as the slightly different ways of achieving the same adaptation by two slightly different, converging stocks. Confidence in this interpretation is encouraged by the fact that a complete and sharp dichotomy of the Coerebidae is possible on the basis of the above differences. Those members which appear to be warblers are *Coereba*, *Conirostrum* and *Ateleodacnis*. Those which appear to be tanagers are *Cyanerpes*, *Chlorophanes*, *Iridophanes*, *Diglossa*, *Hemidacnis*, *Dacnis* and *Euneornis*.

Evidence of Convergence from Plumage Pattern

The writer has not examined *Xenodacnis* or *Oreomanes*, but he presumes them to be nectar-adapted tanagers. Such a presumption is plausible because the suggested dichotomy of coerebid genera is supported by plumage differences. *Coereba*, *Conirostrum* and *Ateleodacnis* have a warbler type of plumage, the other genera a tanager type of plumage, most of them with the same iridescent blues and greens observable in *Calospiza*, a few tending toward the plumbeous blues of *Thraupis*. The bizarre bill of *Diglossa* and unique tongue of *Euneornis* might cast doubt on this simple picture but the division is supported by muscle-pattern and the relief pattern of the horny palate. Moreover, there is no reason to think either that a single warbler genus and a single tanager genus gave rise to nectar-adapted warblers and tanagers, or that the nectar-adapted forms are all equally adapted to the same flowers. As will be shown beyond, the adaptation has apparently occurred in far-removed cases (*Hylophilus poicilotis* is a nectar-adapted vireo that escaped inclusion in the Coerebidae) and

it is partially achieved in warblers and tanagers never included in the Coerebidae.

Regarding the reliability of plumage as an indicator of relationship, studies of the American orioles (Beecher, 1950) show that species are not generally under strong selection pressure to change plumage pattern once this pattern has reached a state of adaptive adjustment to the environment. If the environment changes greatly, plumage tends to evolve rapidly in re-adjustment. Applying this to the present group, there appears to be no reason why tanagers taking up nectar-feeding should change the plumage facies drastically. Since they have not, despite structural changes in the head region accompanying diet specialization, changed their environmental niche, there is no reason for expecting this plumage to change much. The same applies to nectar-specialized warblers: they may logically be expected to retain warbler plumage patterns. Only when change in feeding habit requires change in habitat, as in the derivation of buntings (Emberizinae) from the Parulidae, may rapid and drastic plumage changes be expected.

Evidence of Convergence from the Horny Palate

Sushkin (1927: 3) was impressed with the value of the relief pattern of the horny palate in diagnosing large groups. This character, not to be confused with the bony palate as seen in cleaned skulls, is apparent in the roof of the upper mandible of bird skins prepared with the bill open or in alcoholic specimens. As shown in Figure 4, there are three distinct ridges on the horny palate of both warblers and tanagers, and the differential emphasis on these in the two groups permits separation of their convergent representatives in the Coerebidae. In tanagers and their nectar-adapted forms the lateral ridges are strongly emphasized and continuous to the back of the tomium, whereas in warblers and their nectar-adapted forms they are little emphasized and die out posteriorly. The palate, posterior to the central ridge, is flat and virtually without relief in tanagers, vaulted and sculptured in warblers. These features, especially the condition of the lateral ridges, are diagnostic of warblers and tanagers and support the same dichotomy of coerebid genera as has been indicated above by muscle-pattern and plumage.

Evidence of Convergence from the Tongue

If more than one warbler genus and more than one tanager genus evolve nectar-adapted forms, and if these in turn are specialized for particular flower types rather than for all flowers, convergent overlap of bills and tongues is to be anticipated. It is clear that diagnostic distinctions in external bill structure do not occur among the warblers and tanagers feeding on nectar, even though the horny palate and muscle-pattern have in each case passed through this adaptation without loss of their basic characters. In the tongue, which varies considerably even among closely related species of warblers, we should expect

least of all to find conservatism, particularly if there are special adaptations for special kinds of flowers. Here, in fact, we find the least satisfactory means for distinguishing between nectar-adapted warblers and nectar-adapted tanagers because basic distinctions are apparently obliterated by convergent "overlap" of these too-plastic characters.

In general the Hawaiian Drepanididae,² which are almost certainly of tanager origin (Beecher, unpublished), have progressed farther in tongue modification than any coerebid genus. As Lucas (1894: 306) has observed, the tongues of *Himatione*, *Hemignathus* and *Vestiaria* are perfectly tubular, the fimbriated edges actually overlapping. If the bifid tongues of *Cyanerpes* and *Dacnis* continued to curl, instead of simply forming a highly fimbriated half-curl, the result would be the twin tubes of the *Diglossa* tongue, and this tends to draw all nectar-adapted tanagers together. But there is apparently no sound basis for completely separating the nectar-adapted warblers with their bifid tongues from this broad and variable pattern. It is, however, noteworthy that the whipped out tongue of *Coereba* is remarkably similar to that of the oriole

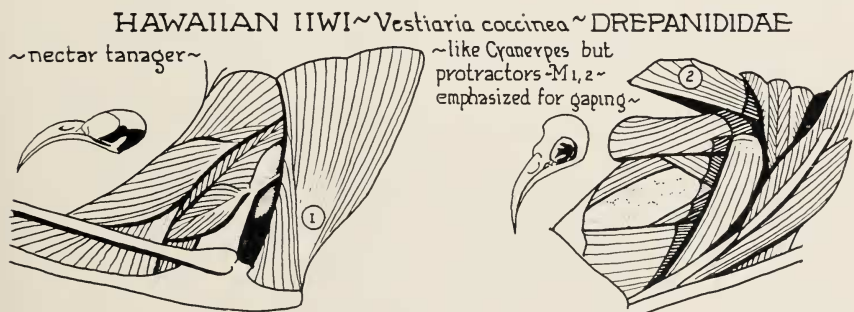


FIG. 5. Jaw muscle-pattern of *Vestiaria coccinea* of the Drepanididae, showing similarity to *Calospiza* and *Cyanerpes* despite development of *M1* and *M2* for gaping.

Bananivorus cucullatus (Beecher, 1950). Both are believed to arise from the warbler phyletic line, the emberizine finches being ancestral to the blackbirds (Icteridae), so this is apparently a case of common stock accomplishing the same adaptation twice in about the same way. The tongue of *Euneornis* is unique and, without histological sections, it is not even quite clear how it functions. But the bird is a tanager on the basis of jaw muscles and horny palate, and probably closely related to *Loxigilla*, which it resembles in these features and even in plumage pattern. Both genera occur in Jamaica, to which *Euneornis* is restricted, and it is possible that the finch *Loxigilla* arose from this tanager. Plumage change might not be expected since Gosse (1847) states that both inhabit the same niche (forest) there.

² Spelled also Drepaniidae and Drepanidae. See review of Amadon's "The Hawaiian Honeycreepers (Aves, Drepaniidae)" in this issue of the *Bulletin*, and also the comments of Ernst Mayr (1943. *Condor*, 45: 46) on the matter.—Editors.

Evidence of Convergence from the Bill Notch

The bill notch is so widespread in passerines that one is forced to conclude that this is a general adaptation for grasping slippery prey and, therefore, not likely to persist in flower probers. In vireos the bill is strongly notched, its shrike-like cast reaching full expression in the tribe Cyclarhini. In tanagers, which may well have arisen from ancestral vireos, the bill is also strongly notched, becoming shrike-like in *Lanio*. But in the warblers, also apparently evolved from vireos, it is weakly notched or un-notched. In *Coereba*, *Conirostrum* and *Ateleodacnis*, here regarded as nectar-adapted warblers, the bill is warbler-like and in the nectar-adapted tanagers—*Dacnis*, *Chlorophanes*, *Cyanerpes*, *Hemidacnis* and *Euneornis*—the bill is tanager-like, generally. But in some of the latter it is doubtfully notched and there is so much individual variation that one cannot safely say a particular genus is notched or not.

Again we find adaptive overlap of too-plastic characters, susceptible to obliteration by the suspected convergence, and it is plain that the bill-notch cannot be used to segregate warblers and tanagers in the Coerebidae. In support of the view that the notch easily disappears in nectar-adapted tanagers we have the evidence that it has done so in some species of the nectar-adapted vireo, *Hylophilus*.

DISCUSSION

Is submergence of the family Coerebidae and the assignment of its genera among the warblers and tanagers justified? Here it should be appreciated that—if both warblers and tanagers arose from vireos—the two families would no sooner have established distinctions through evolutionary divergence than they would, through adaptive convergence, have begun to lose them. The differences to be looked for will not, therefore, be very dramatic and convergent obliteration may be expected especially in the very plastic bill and tongue which fall strongly under selection pressure in nectar-feeding.

The considerable within-the-genus differences of tongues in both the Parulidae and Thraupidae (Gardner, 1925) and of tongues and bills in the Icteridae (Beecher, 1950; 1951) suggest the unreliability of these characters. On the other hand, the constancy of the jaw muscle-pattern in the Icteridae, despite great modification of bill and tongue among the genera, and the conservatism of the pattern of the horny palate, inspire confidence. The latter characters have not only permitted the linking of tanagers to richmondine and cardueline finches but also of warblers to emberizine finches and the latter to the Icteridae. This is not the place to detail these relationships, but characters capable of retaining their essential features through such adaptive transformations of skull and bill can be used with assurance in the present problem.

It is these highly dependable characters of jaw muscle-pattern and horny palate relief that accomplish the division of the genera of the Coerebidae among

the warblers and tanagers—and this in good agreement with plumage pattern. The variable bill and tongue characters overlap adaptively. It is therefore concluded that, in view of the relatively meager diagnostic differences expected in convergent genera arising from groups as closely related as warblers and tanagers, the evidence is sufficient to justify submerging the family Coerebidae.

This seems entirely reasonable. Nectar-feeding has been acquired independently in many American passerine groups: vireos, warblers, tanagers, blackbirds and even finches—not to mention derived groups like the geospizids of the Galápagos and the drepanidids of the Hawaiian Islands. Various degrees of adaptive modification for the trait are seen, not only in the bills and tongues but also in relative development of jaw muscles. In fact two distinct mechanical adaptations may be distinguished in the nectar-feeders of the Thraupidae and Parulidae and this may be regarded as an additional diagnostic difference.

The nectar-adapted warblers are “gapers” (Beecher, 1950; 1951). As noted for *Coereba* in Figure 2, *M. depressor mandibulae* (*M1*) is highly developed in both *Conirostrum* and *Ateleodacnis*. The bill is apparently plunged into a flower closed, then opened forcefully to spread the flower parts and permit the tongue to reach the nectar—or possibly a hole is pecked in the side of a flower and enlarged in this manner. Functionally it is the same adaptation noted in the Icteridae and in the Old World Sturnidae, with a lever-like posterior extension of the mandible. In Figure 2 *Coereba* is compared with *Oporornis*, which shows the same adaptation, though not all warblers are gapers in this degree.

The Neotropical nectar-adapted tanagers are non-gapers. In none of them is *M1* more highly developed than in *Cyanerpes* (Fig. 2), and it is apparent that these species simply insert the bill into flowers and sip nectar. *Diglossa* has been observed by Moller (1931: 292) to tear a hole in the side of a tubular corolla with its short, hooked bill to get at the nectar it could not otherwise reach.

However, the tanager stock apparently can produce gapers. In the nectar-adapted drepanidids, *Vestiaria coccinea* (Fig. 5), *Himatione virens*, and *Hemignathus lucidus*, the origins of protractors *M1* and *M2* are greatly expanded for gaping in tubular corollas, and the adductors *M6* and *M7* are greatly reduced. Otherwise these birds are very similar to *Calospiza* or *Cyanerpes*. That the drepanidids have a tanager origin is supported also by the identity of muscle-patterns in the Hawaiian finch, *Psittirostra cantans*, and the cardueline finch, *Carpodacus mexicanus*. This may be interpreted as two independent origins of nearly identical finches from a common tanager ancestor.

As for *Spodiornis rusticus*, Wetmore and Phelps (1949: 378) observed that “the form of the tail and of the tongue suggest affinities with the Coerebidae, . . . the family in which P. L. Sclater originally described *Spodiornis*.” The palate of *Spodiornis* suggests relationships with primitive emberizine finches

like *Phrygilus*, however, and this may be one of those rare compromises—an intermediate between nectar-adapted warbler and emberizine finch. The highly angulated commissure of nectar-feeders, correlated with forward vision, is thought to pre-adapt them for seed-cracking before the bill becomes too long.

This paper has concerned itself with the submergence of the family Coerebidae as an unnatural category and the re-assignment of its genera among the warblers and tanagers. Some ornithologists will wish to retain this family name for some part of the group. There appears to be no valid reason for so doing, though the nectar-adapted warblers might be known as the tribe Coerebini and the nectar-adapted tanagers as the tribe Dacnini.

But nectar-feeding in the American nine-primaried assemblage should not be over-emphasized. Numerous references to the sucking of fruit and flower juices by warblers and tanagers never included in the Coerebidae could be cited. In the present state of our knowledge it would be difficult to know which ones to include in these tribes—unless we settle upon the genera dealt with above for the time being. Nectar-feeding is a general trait of the Thraupidae, Parulidae, Vireonidae, Icteridae, and even the polyphletic "Fringillidae." No useful purpose is served by giving it too much recognition in the classification of these higher categories.

SUMMARY

An attempt is made on the basis of anatomical material, to show that the neotropical Honey Creepers (Coerebidae) are an artificial group composed of nectar-adapted warblers and nectar-adapted tanagers that have become convergently similar due to similar diet. Considerable care is taken to select for comparison anatomical characters likely to have been modified but little by such convergence. This precaution is necessitated by the close relationship of the warbler and tanager families due to their apparent common origin from ancestral vireos. Evidence from jaw muscle-pattern and horny palate relief is given special weight because of the constancy of these features in other passerine families studied anatomically. Tanagers and warblers have distinctly different patterns for both characters and it has been found that a clean separation of the Coerebidae into nectar-adapted warblers and nectar-adapted tanagers is possible. This dichotomy is in good agreement with plumage differences, the latter group having tanager plumage, the former, warbler plumage. A functional difference in the manner of feeding on nectar is also in agreement with this division. Such characters as bill shape and tongue specialization overlap convergently and are unreliable.

On the basis of this analysis it is concluded that the family Coerebidae should be submerged as an unnatural group, and its genera distributed among the warblers and tanagers. The genera *Coereba*, *Conirostrum* and *Ateleodacnis* could be regarded as a nectar-specialized tribe of the Parulidae—the Coerebini. The genera *Diglossa*, *Cyanerpes*, *Chlorophanes*, *Iridophanes*, *Hemidacnis*, *Dac-*

nis and *Euneornis*, and probably also *Xenodacnis* and *Oreomanes*, could be regarded as a nectar-specialized tribe of the Thraupidae—the Dacnini.

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